ECOLOGICAL ANALYSIS OF THE LIVING MOLLUSCS OF THE TEXAS PANHANDLE

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ABSTRACT

The living molluscan fauna of the Texas Panhandle includes a total of 43 species: nine freshwater gastropods, 24 terrestrial gastropods (including one slug), and ten freshwater bivalves. Except for one terrestrial gastropod and one bivalve, all of these species are native to the central United States. Five freshwater and seven terrestrial gastropods, and six freshwater bivalves are here reported living in the Texas Panhandle for the first time. One terrestrial gastropod is a new record for Texas. Occurrence of freshwater gastropods and pelecypods is limited by quality and quantity of surface waters, whereas terrestrial gastropods are limited by distribution of surface soil moisture and cover objects. Highest diversity terrestrial faunas are associated with woodlands of plains cottonwood, *Populus sargentii*, but the mesic-adapted species can be found in moist floodplains even in the absence of trees.

Until recently, the living molluscan fauna of the Texas Panhandle has been poorly known. General biological interest in this area has been limited in the past, at least partially because of a presumed low species diversity. The Texas Panhandle presents an extreme environment for both terrestrial and freshwater molluscs. The general aridity of the climate is made even more rigorous for molluscs by wide seasonal thermal extremes. For this study, the Texas Panhandle was defined as that part of Texas between the 100th and 103rd meridians and north of 34°18'40''N, corresponding to a series of county boundaries between Cottle/Childress on the eastern end and Bailey/Parmer on the western end (Fig. 1).

STUDY AREA

Two major physiographic regions exist in the Texas Panhandle. The greater part of the area is within the High Plains where Quaternary eolian deposits overlie the Ogallala Formation of the Miocene and Pliocene. The High Plains is a nearly level plain rising gradually to the west. Potential natural vegetation for most of the Texas Panhandle is short and mixed grass prairies as observed by early European explorers (Strout, 1971; Flores, 1984). Woody plants were few in species number and were generally restricted to canyons and steep slopes (Palmer, 1920).

The eastern portion of the Panhandle is the second physiographic region and contains a mosaic of two units: 1) Permian redbeds or "badlands" with limited soil development and a mixed grassland/scrub community; 2) Quaternary alluvial plains with deep soils that naturally supported mixed grass prairie communities. The Permian badlands extend westward along the Canadian River. Gallery woodlands exist on Quaternary alluvial deposits along the larger water courses. Portions of the northeastern and southwestern Panhandle contain sand hills and ridges overlying the Ogallala and support a mixed grass/herbaceous prairie community or a stunted woodland community.

Analysis of the herpetofauna and woody flora reveals a mixed biota with regard to biogeographical affinities of the constituent species. Species present include those characteristic of central prairies, southern savannahs and brushlands, and western montane areas along with a few representatives of eastern forests (Palmer, 1920; Fouquette and Lindsay, 1955).

The Texas Panhandle has a warm temperate, semiarid, continental climate. Mean annual temperature at Amarillo is 13.9°C, with record extremes ranging from −26.7°C to 41.1°C. The growing season averages 190 days from 17 April to 24 October. Summer days produce high temperatures (64 days with maximum above 32.2°C), but radiational cooling results in cool nights and early morning hours. Winter weather is characterized by strong cold fronts with occasional blizzards, but these fronts are usually followed by a warming trend after several days. Freezing temperatures occur on 110 days annually. Average annual precipitation is 485 mm with a record of 1110 mm in 1923. Most precipitation occurs during thunderstorms, which occur on an average of 49 days annually. The above climatic data are taken from the Natural Fibers

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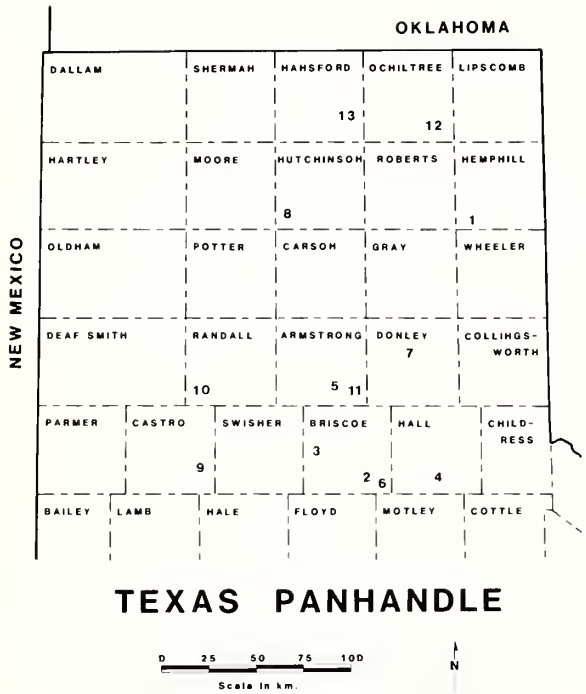

Fig. 1. Panhandle of Texas giving collection localities referred to in text.

Information Center (1987).

The Texas Panhandle is drained by the Red/Canadian drainages of the Mississippi River system except for the extreme southwestern corner which is drained by Running Water Draw of the Brazos River drainage. Flowing waters in this region are quite restricted in width, depth, and permanence. Large streams have low flows with high concentrations of suspended red silt/clay and dissolved salts. Such water conditions are natural (E. James *In:* Thwaites, 1905), but modern land use practices have further decreased the water quality of these streams. Water flows in these larger streams have been described as being "either dry or raging current" (Gould, 1906:42). Small feeder creeks are generally intermittent but a few creeks have perennial flows supplied by "sweetwater" springs supplied by the Ogallala Aquifer. Natural lakes are limited to the numerous playas on the High Plains surface (Guthery and Bryant, 1982).

LITERATURE REVIEW

Neck (1984) published the results of a survey of living terrestrial gastropods of various canyons of the Eastern Caprock Escarpment. Most published records (Henderson, 1909; Strecker, 1910; Walker, 1915; Clarke, 1938) were rejected as being samples of flood debris containing shells of undeterminable, probably fossil, origin. Only a few published records of gastropods from this area were accepted as representing modern living populations (Pratt, 1965; Metcalf *In:* Franzen, 1971; Metcalf *In:* Bequaert and Miller, 1973). The opinions of Neck (1984) and the records accepted therein produced a list of 12 species of terrestrial gastropods known to be living along the Eastern Caprock Escarpment; two additional species were known from other areas of the Texas Panhandle.

A subsequent review of terrestrial gastropods of the eastern United States (Hubricht, 1985) included several new records from the Texas Panhandle. The reports of *Vallonia pulchella* (Müller), *V. cyclophorella* (Sterki), and *V. perspectiva* Sterki from Potter and Randall counties (Hubricht, 1985:63, 65, 67) probably represent reworked fossil shells or introduced populations (Pilsbry, 1948; Bequaert and Miller, 1973; Pierce, 1975; Neck, 1989a) and are not accepted as native members of the living Panhandle fauna. Only limited records of urban molluscs of the Texas Panhandle are available (Neck, 1989a). Hubricht (1985) reported *Succinea forsheyi* I. Lea and *S. indiana* Pilsbry from Hemphill and Sherman counties, respectively, although taxonomic uncertainty prevents complete udnerstanding of species relationships of the succineid snails. The Sherman County record was originally referred to *S. vaginacontorta* Lee by Franzen (1971), a taxon synonymized with *S. indiana* by Hubricht (1985).

Records of freshwater gastropods from this area are also rare (Fullington, 1978), although *Physella* sp. and *Planorbella* sp. were observed in playas as early as 1876 (E. H. Ruffner *In:* Baker, 1985). Clarke (1938) reported *Physella virgata* (Gould) living in "Paladura Creek [northeast] of Canyon," which is actually the Palo Duro Canyon of the Prairie Dog Town Fork of the Red River. Singley (1893) reported *P. virgata* and *Planorbella trivolvis* (Say) from a playa. Strecker (1910) reported *P. virgata* and *P. tenuis* (Dunker) from creeks and tanks in Armstrong County. A survey of playa lakes of the Llano Estacado of Texas and New Mexico (Sublette and Sublette, 1967) revealed the presence of *P. trivolvis* in five of 12 playas surveyed in the current study area. Rhodes and Garcia (1981) reported "snails (mostly *Physa* sp. and *Lymnaea* sp.)" from all eight playas that they surveyed from Castro and Swisher counties. Neck (1982) reported *P. virgata* and *P. trivolvis* from Lake Theo, Briscoe County. Several freshwater gastropods have been reported from playas in Castro County (Neck and Schramm, in press).

Freshwater bivalves are less widely distributed in the Texas Panhandle than are freshwater gastropods. Clarke (1938) reported living *Sphaerium striatinum* (Lamarck) [as *S. sulcatum* (Lamarck)] and *Uniomerus tetralasmus* (Say) from the Prairie Dog Town Fork of the Red River, Randall County. The occurrence of *U. tetralasmus* in a stream of variable volume is related to the ability of this species to withstand complete desiccation of its habitat. Neck (1982) reported *S. striatinum* and an introduced population of *Anodonta grandis* Say in Lake Theo, an artificial impoundment on Holmes Creek, Caprock Canyons State Park, Briscoe County. Populations of the widespread exotic Asian clam, *Corbicula fluminea* (Müller), occur in Greenbelt Reservoir, Donley County, and Lake Meredith, Hutchinson County (Neck, 1987b). A single record of *S. striatinum* from a playa is known (Neck and Schramm, in press).

METHODS AND RESULTS

Soil or benthic samples were either obtained by the author or received from other field workers as noted. Mollusc

Table 1. Occurrence of living nonmarine molluscs in the Texas Panhandle (includes both published reports and reports herein): O = previously published reports of living terrestrial accepted by Neck (1984); A = records in Singley (1893); B = Strecker (1910); C = Clarke (1938); S = Sublette and Sublette (1967); F = Fullington (1969, 1978); N2 = Neck (1982); N4 = Neck (1984); H = Hubricht (1985); N7 = Neck (1987b); NS = Neck and Schramm, in press; U = urban snails in Neck (1989*a*); single numbers refer to locality numbers in text; taxa are presented in phylogenetic sequence within each group.

Species	O	A	B	C	S	F	N2	N4	H	N7	NS	U	1	2	3	4	5	6	7	8	9	10	11	12	13
FRESHWATER GASTROPODS																									
Hebetancylus excentricus													X												
Fossaria cockerelli											X						X								
F.dalli																								X	
F. modicella																			X						
F. parva													X												
Physella virgata		X	X	X		X	X			X	X		X			X		X	X	X	X	X	X	X	
Gyraulus parvus						X					X							X							
Planorbella tenuis			X			X				X			X	X			X		X		X			X	
P. trivolvis		X			X		X				X											X			
TERRESTRIAL GASTROPODS																									
Vallonia gracilicosta	X							X							X							X		X	
V. parvula	X							X	X	X			X						X			X	X	X	
Pupoides albilabris								X	X					X	X				X			X	X	X	
Gastrocopta cristata								X	X			X	X	X	X						X	X		X	
G. pellucida								X	X				X	X					X			X	X	X	
G. procera								X					X	X					X			X	X	X	
G. armifera								X	X				X						X			X	X	X	
G. abbreviata									X						X				X					X	
G. tappaniana													X						X						
Vertigo ovata															X				X						
Succinea forsheyi									X															X	
S. indiana	X								X										X			X			
Catinella cf. avara								X					X						X		X			X	
Oxyloma retusa																		X							
Helicodiscus parallelus								X														X		X	
H. singleyanus																						X	X	X	
H. inermis								X	X				X	X	X				X						
Deroceras laeve								X							X				X		X			X	X
Hawaiia minuscula																								X	
Zonitoides arboreus																						X			
Euconulus trochulus													X		X				X					X	
Rumina decollata												X													
Rabdotus dealbatus	X							X	X													X			
Stenotrema leai	X								X																
BIVALVES																									
Anodonta grandis							X											X		X				X	
A. imbecilis																				X					
Uniomerus tetralasmus				X																		X			
Sphaerium striatinum				X			X				X						X								
Musculium transversum																								X	
Pisidium casertanum																		X						X	
P. compressum																		X							
P. nitidum																								X	
P. punctiferum																								X	
Corbicula fluminea										X										X					

shells were extracted by hand picking and screening with soil sieves (nested series of #4, #8, #16, and #30) and identified. Below is a description and location of each collecting site with a statement of the significance of recovered species. Species recovered in the current study as well as those from previously published reports are tabulated in Table 1. Species for which living representatives are recorded for the first time from the Texas Panhandle are discussed below (see appendix 1).

LOCALITIES

Locality 1. Modern alluvium of Washita River at U.S. 83, 21.4 km south of Canadian, Hemphill County; area with grasses, shrubs at 770 m elevation; sampled 5 Apr 1984. Soil samples

were taken from underneath downed wood. *Fossaria parva* (Lea), *Hebetancylus excentricus*(Morelet), *Gastrocopta tappaniana* (C. B. Adams), and *Euconulus trochulus* (Reinhardt) from this site were reported living in the study area for the first time. Also significant in this collection was the occurrence of *Gastrocopta armifera* (Say) in an herbaceous community; previously, this species had been found in the Texas Panhandle only in habitats dominated by trees with abundant leaf litter on soil surface.

Locality 2. Terrace surface above South Prong of Little Red River, 1 km northwest of Eagle's Point, Caprock Canyons State Park, Briscoe County, at 710 m elevation; sampled 6 Apr 1984. Soil samples were taken from underneath downed wood or juniper duff in redberry juniper - mesquite (*Juniperus pinchotii* Sudworth - *Prosopsis glandulosa* Torrey) scrub. All species in Table 1 under column 2 were found in soil samples taken from underneath downed wood; *Pupoides albilabris* (C. B. Adams) was not found in the sample from juniper duff lacking downed wood (underneath same *J. pinchotti*).

Locality 3. Canyon of East Fork of Rock Creek (Tule Creek drainage), 3.2 km north of Texas 86, 11 km west of Silverton, Briscoe County, at elevation 960 m; sampled 8 Apr 1984. Sample site was a small side canyon off right bank with seeps and abundant leaf litter of plains cottonwood *(Populus sargentii)* over colluvium derived from Pleistocene Tule Formation overlying Triassic sediments. *Vertigo ovata* Say was previously unknown living in study area; only other record of living *E. trochulus* in the study area was Locality 1 (see above). Also significant were the occurrences of the gray slug, *Deroceras laeve (Müller), and Gastrocopta abbreviata* (Sterki). *D. laeve* was collected as eggs that later hatched in laboratory.

Locality 4. Hancock Lake, natural lake occupying a subsidence basin (doline), 31 km WSW of Memphis, Hall County, at 623 m elevation; sampled 11 Jul 1984 by S. C. Caran. Living aquatic snails *(Physella virgata)* were collected from depth of less than ten cm; substratum was black, sapropelic (extremely humic), silty to fine sandy clay with strong sulfurous odor. This was first record of living aquatic snails in a natural lake (a doline differs from a playa in geological origin) in study area.

Locality 5. Playa crossed by Texas Highway 217, 3.8 km east of junction with FM 1541, south side of road, Randall County, at 1090 m elevation; sampled 26 Mar 1986 by S. C. Caran. Specimens (all freshwater snails) included first living *Fossaria cockerelli* Pilsbry and Ferriss from the Texas Panhandle. Other species present was *Planorbella tenuis* which has a fine-sculptured shell and is nominally separable from *P. trivolvis*.

Locality 6. Lake Theo, artificial impoundment on Holmes Creek in Caprock Canyons State Park, Briscoe County; two samples.

Sampling of desiccated cattail *(Typha)* marsh along margins of the upper portion of Lake Theo on 5 Oct 1977 revealed two shells of *Oxyloma retusa* (Lea), a species previously not known to live in Texas (elevation - 785 m). Substratum was a reddish sandy silt that is submerged to a depth of approximately one decimeter at normal high water. No shells of other terrestrial gastropods were observed. Shells of *Physella virgata* and *Planorbella trivolvis* were present at this site, indicating recent periods of inundation.

Sampling of benthos by ponar dredge on 10 Aug 1987 by Greg Conley revealed two species of pea clams [*Pisidium casertanum* (Poli) and *P. compressum* Prime] heretofore not reported from the Texas Panhandle. Both species have been reported from Texas by Herrington (1962) who did not provide specific localities. These pea clams were more abundant in the deepest and middle portions of the lake than in the shallow portion, possibly in response to persistent flow of the natural "sweetwater" springs now inundated by Lake Theo, which contains waters with high levels of gypsum. Other freshwater molluscs recovered in these samples included *Gyraulus parvus* (Say), *Physella virgata*, and *Anodonta grandis* (shell fragments only of the latter species); of these species, all but *G. parvus* reported from Lake Theo by Neck (1982).

Locality 7. Turkey Creek (Salt Fork of Red River drainage), 4.8 km northeast of Green Belt Reservoir dam, Donley County, at 798 m elevation; sampled 4 Oct 1987. Sample sites were stream and terrace (underneath downed wood and bark of cottonwood) adjacent to stream, which at this point was a wide pool with associated marsh *(Typha, Eleocharis, Scirpus)* and localized riparian woodland *(Salix, Populus, Celtis, Cephalanthus). Planorbella tenuis* was common in side pools (10-15 m deep) whereas *Physella virgata* and *Fossaria modicella* (Say) were found in shallow pond margins and isolated pools of nearly stagnant water. Terrestrial gastropod fauna of 12 species in riparian soils was exceptionally diverse for the Texas Panhandle. Especially noteworthy was the occurrence of several regionally rare species - *Euconulus trochulus, Gastrocopta tappaniana, G. abbreviata,* and *Vertigo ovata.* The xeric upland slopes were locally inhabited by *Succinea indiana.*

Locality 8. Bugbee Canyon inlet of Lake Meredith, Canadian River, Hutchinson County, with elevation of reservoir surface at approximately 890 m; sampled 5 Oct 1987 with field assistance by S. C. Caran. This quiet water cove in a reservoir (created in 1965) supported populations of *Corbicula fluminea* (see Neck, 1987b), *Anodonta grandis, A. imbecillis* Say, and *Physella virgata*. The three bivalves were previously unknown from the Canadian River drainage in Texas. *A. imbecillis* had not previously been recorded from the Texas Panhandle.

Locality 9. Tule Creek at FM 2301 crossing (Red River drainage), Swisher County, at 988 m elevation; sampled 22 Oct 1987. A *Scirpus/Typha* marsh encircled deeper, open water and was bordered by clay soil with calcareous cobbles. This locality was significant because the permanent water is the result of natural hydrogeological conditions, not human alterations. Especially significant was the occurrence of the finger-

nail clam, *Sphaerium striatinum*, in a natural waterbody (no other such modern records are known).

Locality 10. Buffalo Lake National Wildlife Refuge, Randall County, sediment from currently dry lake (impounded Tierra Blanca Creek of Prairie Dog Town Fork of Red River drainage) and upland soil samples from calcareous sandy soils developed on slopes of Ogallala Formation at 1120 m elevation; sampled 22 Oct 1987. Dominant plants were side-oats grama (*Bouteloua curtipendula* Michaux), little bluestem (*Schizachyrium scoparium* Michaux), sand bluestem (*Andropogon halli*), narrowleaf yucca (*Yucca angustifolia* Hackel), skunkbush sumac (*Rhus aromatica* Aiton), and three-awn (*Aristida* sp.). The freshwater mussel, *Uniomerus tetralasmus*, had previously been reported from the Texas Panhandle (Clarke, 1938—specimens in USNM, lot #170791, collected 4 Jul 1937; specimens also collected at Buffalo Lake by A. L. Metcalf 29 Jul 1975, un-published—MALB lot #49). *Rabdotus dealbatus* (Say) occurred in a tall grassland on slopes; specimens are whitish with faint coffee-colored base (more similar to many specimens of *R. mooreanus* (Pfeiffer) in central Texas than to specimens of *R. dealbatus* from Caprock Canyons State Park - Neck, 1984). *Zonitoides arboreus* (Say) and the other mesic-adapted terrestrial gastropods from this locality were recovered from deep soil, leaf litter, and bark/wood fragments below eastern hackberry (*Celtis occidentalis* Linnaeus) in a wide draw at the floodpool shoreline of the presently dry Buffalo Lake.

Locality 11. Right bank of Prairie Dog Town Fork of Red River, Palo Duro Canyon Park, Randall County, at 875 m elevation; sampled 6 Dec 1988. Sample site was the stream and a terrace with overflow channel between horse stable and park store. Dominated by plains cottonwood, other plant cover included sand bluestem, Indian grass (*Sorghastrum nutans* Linnaeus), and hackberry. Significant was presence of *Gastrocopta armifera* in a xeric site with only large pieces of downed wood and flood debris as cover; no leaf litter accumulations were present.

Locality 12. Free-flowing and impounded portions (Lake Fryer) of Wolf Creek (of North Canadian River); within, upstream, and downstream from Wolf Creek County Park, Ochiltree County, at 795-815 m elevation; sampled 7 Dec 1988. Sampled vegetation communities included hackberry/cottonwood, cottonwood, willow, and Rocky Mountain juniper woodlands. Sites included water courses, extremely mesic stream banks, well-drained slopes, and well-drained terrace. Significant aquatic records included the first records in study area of *Pisidium punctiferum* (Guppy), *P. nitidum* (Jenyns), *Musculium transversum* (Say), and *Fossaria dalli* (F. C. Baker), as well as the first native occurrence of *Anodonta grandis* (as indicated by the occurrence of nested pairs of shells in prehistoric archeological sites). Terrestrial samples yielded first record of *Hawaiia minuscula* (A. Binney) in area, additional records of *Helicodiscus singleyanus* (Pilsbry) and *Euconulus trochulus*, and micro-sympatric occurrence of *Gastrocopta armifera* and *G. abbreviata*.

Locality 13. Drainage of Palo Duro Creek of North Canadian River (within future limits of Palo Duro Reservoir), northeast of Spearman, Hansford County, at 860 m elevation; sampled 7 Dec 1988. At confluence of Palo Duro Creek and Horse Creek, an overmature plains cottonwood riparian woodland with much downed wood on deep sand revealed only *Deroceras laeve*.

DISCUSSION

COMPLETENESS OF FAUNAL SAMPLING

In general, the report of additional species (see appendix 1) from the Texas Panhandle resulted from surveys of previously unsampled habitats. These newly-sampled habitats had enviornmental characteristics (physical or biological) that allowed survival of a different suite of species or have zoogeographical dispersal routes available from difference source areas. The only definitely introduced molluscs reported from the Texas Panhandle were one gastropod, [*Rumina decollata* (Linnaeus)] and one bivalve *(Corbicula fluminea)*. Undoubtedly, other introduced gastropods were established in urban areas, but these habitats have not been sampled adequately at this time (but see Neck, 1989a). The populations of *Oxyloma retusa, Anodonta imbecillis*, and *Pisidium compressum* should be considered recent introductions via migratory waterfowl until native populations in natural habitats, i.e non-reservoir sites, are located. These species are not native in the strictest sense of the term, but neither have they been introduced deliberately or even indirectly by human activities. The habitats required by these aquatic and amphibious species are not represented in the Texas Panhandle except in areas modified by human activity.

Sampling of additional sites with dependable, i.e. permanent, water supplies, and/or protection from intense summer solar insolation could reveal additional species to be living in this area, although "the number to be expected is very low" (Neck, 1984). However, certain habitats have been sampled sufficiently that additional species are unlikely to be recovered from these areas. The xeric scrub in the "badlands" along the eastern margin of the Caprock Escarpment is a harsh environment for land snails. Dominated by mesquite and red-berry juniper, this community is characterized by limited humus development, exposure to extremes of temperature, and susceptibility to soil erosion. Collections at Caprock Canyons State Park (locality 2) revealed that several species of land snails can survive in the limited humus available under junipers in the absence of downed wood. However, only species previously reported from this habitat were recovered.

Additional species are known from areas immediately south of the Texas Panhandle. Sublette and Sublette (1967) reported *Fossaria bulimoides* from three to nine playas surveyed on the Southern High Plains of Texas and New Mexico south of the present study area (but see reference to this taxon in subsection on Nomenclatural and systematic compilations). Fullington (1978) reported the tropical/semitropical aquatic snail *Biomphalaria havanensis* (Pfeiffer, 1839) from Garza and Scurry counties in the southern Rolling Plains.

Pierce (1975) reported several "modern faunas" from drift samples from Lynn County, south of the Texas Panhandle. Two species not known living in the Texas Panhandle were listed from these samples. *Pupilla blandi* E. S. Morse ("dried flesh in several shells") and *Vertigo gouldi* (A. Binney) ("very fresh and unweathered") were allegedly documented as living. Populations of these two species as well as species known from adjacent counties of adjoining states could also occur in the Texas Panhandle.

Although only limited records of molluscs had been reported in the Texas Panhandle prior to the current series of field studies, additional surveys have been accomplished in areas north of the Texas Panhandle. Surveys of several counties in southwestern Kansas have indicated the occurrence of significant but low-diversity molluscan faunas (Leonard, 1943; Branson, 1972). Several additional species not known to live in the Texas Panhandle have been reported living in Cimarron County, in the Oklahoma Panhandle (Metcalf, 1984). Three species—*Gastrocopta holzingeri* (Sterki), *Pupilla muscorum* (Linnaeus), and *Pupoides inornatus* Vanatta—are known from basaltic talus (a microhabitat not present in the Texas Panhandle) and may owe their occurrence in Cimarron County to periodic immigration from upstream populations in the Sangre de Cristo Mountains of northern New Mexico and southern Colorado, or in basalt fields of northeastern New Mexico.

The apparent absence of at least one freshwater gastropod from the Texas Panhandle is significant. *Helisoma anceps* (Menke) is a common species in Pleistocene fossil assemblages from this area. Living populations of *H. anceps* are known from the Hill Country of Texas on rocky substrates (bedrock or gravel). This habitat is not present in the Texas Panhandle at present. Elsewhere in North America, *H. anceps* may be found in lakes, ponds, rivers, and streams with vegetation on various substrates in permanent water (Clarke, 1981). Sufficient areas of this habitat do not occur in the Texas Panhandle today; otherwise *H. anceps* could be present.

NOMENCLATURAL AND SYSTEMATIC COMPLICATIONS

Even if faunal sampling efforts were considered to be reasonably complete, ecological analysis of the fauna is dependent upon the state of systematic and nomenclatural knowledge and stability. The application of proper scientific names to certain molluscan taxa of the Texas Panhandle is complicated by a lack of detailed taxonomic knowledge. The general uncertainty associated with proper identification of taxa of the family Succineidae has been mentioned earlier, as has the close relationship between *Planorbella trivolvis* and *P. tenuis*. Also unclear is the separate status of *Fossaria cockerelli* (listed in Table 1) and *F. bulimoides* (mentioned in previous subsection). Part of the doubt concerning these latter two pairs of species is caused by changes in perceived systematic status through time. Analysis of published records of these taxa is complicated because of the unavailability of reference specimens.

Very few records of modern *Gastrocopta abbreviata* have been reported from Texas. The original record by Pilsbry (1948) has been suspected (and rightly so) of being a fossil drift specimen (Cheatum and Fullington, 1973). Hubricht (1985) listed a record from Potter County. The relationship of *G. abbreviata* to its very closely related congener, *G. armifera* (Say, 1821) has been unclear, although Hubricht (1972) demonstrated slight but distinctive differences between these two forms. Turkey Creek (locality 8) was the first reported micro-sympatric occurrence of living populations of these two species in Texas, although co-occurrence in fossil assemblages in central Texas was reported by Hubricht (1972). Co-occurrence of living *G. abbreviata* and *G. armifera* has been reported in Missouri, Mississippi, Oklahoma, and Kansas (Hubricht, 1972).

Subsequent systematic studies could alter the perceived relationships of some or all of these closely related taxa. Such changes could alter the exact number of species recognized in total or within any of several ecological communities. However, the environmental settings of these populations are now known. Therefore, an ecological analysis of the modern native molluscan fauna of the Texas Panhandle is presented below.

MOLLUSCAN COMMUNITIES OF TEXAS PANHANDLE

The major factor controlling species diversity of living molluscs in the Texas Panhandle is reliable water. A dependable water supply provides a medium in which aquatic gastropods and bivalves can live. Additionally, water also allows development and maintenance of trees that produce leaf litter, downed wood, and shade, which conserve soil moisture and ameliorate the devastating effects of direct solar exposure upon terrestrial gastropods.

Several community types of aquatic molluscs can be recognized in the Texas Panhandle. Perennial creeks without excessive loads of dissolved solids are occupied by *Gyraulus parvus, Planorbella tenuis, Fossaria cockerelli,* and *Hebetancylus excentricus*. Playas and stockponds typically have *Physella virgata, P. trivolvis* (and occasionally *P. tenuis*), and *G. parvus* (latter species typically restricted to certain playas). Intermediate and large reservoirs contain many of the above species in protected coves, but also can contain the bivalves *Anodonta grandis, A. imbecillis, Corbicula fluminea,* and *Sphaerium striatinum*. Several species of pea clams (*Pisidium* spp.) are known from this area, but the limiting ecological factors are not understood.

A predictable suite of terrestrial gastropods is characteristic (but not restricted to) upland, well-drained microhabitats that represent the most extreme xeric conditions that are tolerated by terrestrial gastropods in the Texas Panhandle. The fauna of this upland community consists of varying proportions of the following species: *Pupoides albilabris, Gastrocopta procera* (Gould), *G. pellucida* (Pfeiffer), *G. cristata* (Pilsbry and Vanatta), and *Helicodiscus inermis* H. B. Baker. These species can withstand lengthy periods of drought with minimal cover. Thick leaf litter suffices as minimal cover for all of the above species except for *P. albilabris* which requires additional cover in the form of downed wood.

The more mesic-adapted terrestrial gastropods of the Texas Panhandle can be readily divided into two communities. The more drought resistant of these species (*Vallonia parvula* Sterki, *V. gracilicosta*, and *Gastrocopta armifera*) survive in well-drained habitats if sufficient cover in the form of rocks, downed wood, or thick leaf litter occurs at the site. These species are adapted to microhabitats that conserve maximum percentages of the moisture supplied by local precipitation, including that falling immediately upslope. The less drought-resistant of the mesic-adapted species (*Vertigo ovata, Euconulus trochulus, Gastrocopta tappaniana,* and *Deroceras laeve*) are able to survive drought periods only in microhabitats which obtain moisture input in addition to local precipitation. Such additional soil moisture could represent ground-water seepage or floodplain wicking of surface stream water. Often both of the above communities occur together in bottomland habitats with additional moisture input.

PLAINS COTTONWOOD AS A HABITAT INDICATOR

The downed wood that is a major moisture conservation agent for terrestrial gastropods in the Texas Panhandle is almost invariably from plains cottonwood, *Populus sargentii* Dode, or common hackberry, *Celtis occidentalis*. *P. sargentii* is the most abundant source of downed wood in streamside habitats. Although willows, *Salix* sp., are present along some streams, downed wood from willow often occurs in the stream and does not provide suitable habitat for terrestrial gastropods. *C. occidentalis* normally occurs at a slightly higher elevation above the stream than *P. sargentii*, but the former species supplies downed wood, which provides sufficient cover for most of the more drought resistant species of the mesic-adapted fauna.

Populus sargentii is not an absolute indicator of the existence of the most mesic-adapted gastropod community, because it can occur in well-drained sites that support only the xeric-adapted gastropod community; Neck (1984) noted occurrence of only *Pupoides albilabris* and *Gastrocopta cristata* (Pilsbry and Vanatta) at locality B-1, a site on the floodplain of an intermittent stream, the South Prong of the Little Red River, which exhibits high variation in stream flow with minimal surface water for the major part of the year. At this site, the soil is typically desiccated allowing the existence of a low diversity terrestrial gastropod fauna that contains only the xeric-adapted species. Only a slug, *Deroceras laeve*, which is able to burrow deeply to subterranean moisture sources, can survive in the deep sands at locality 13 even though a thick stand of *P. sargentii* and much downed wood exists at this site.

Populus sargentii is also the dominant tree species on floodplains of large streams such as the Canadian River. At these sites, large trees exist in a parkland community with only limited understory vegetation. No molluscan samples have been obtained from such large-stream floodplain environments. Surface water levels in such habitats are extremely variable—from absent to high (during massive flood events).

The mesic-adapted terrestrial gastropod community appears to require a sufficient depth of sandy soil to provide a subsurface "moisture bank." Terrestrial gastropod faunas with the greatest percentage of mesic species exist in *Populus sargentii* woodlands on floodplains of perennial creeks which have constant, high levels of soil water. Sites of this type (Turkey Creek at locality 7 in this study) support a high-diversity fauna that contains most of the living terrestrial gastropods of this region except for those that require well-drained soils. Sites that are characterized by low-volume but rather constant soil water levels, e.g. the seep at locality 3 of this study, support a moderate-diversity fauna dominated by mesic-adapted species.

The germination requirements of *Populus sargentii* include bare or disturbed sand or fine gravel in full sunlight with few or no plant competitors (Read, 1958; Everitt, 1968). Survival of seedlings and saplings is dependent upon shallow ground water. Old trees could survive some distance from the current stream location as long as the increased relative elevation (resulting from downcutting of the stream) does not preclude tapping of shallow ground water by the root system.

Terrestrial gastropods, however, are dependent upon the presence of cover objects (rock, wood, leaf litter, etc.), which extend the time period that soil moisture levels are conducive to gastropod activity. Soil moisture levels in the Texas Panhandle are adequate below seeps and on low floodplains where surficial flow and subsurface wicking exists. High floodplain flats and sandbars do not normally contain high soil moisture levels. Although large *Populus sargentii* can survive on ground water, terrestrial gastropods must have high surface soil moisture levels. The direct importance of soil moisture and cover objects is well illustrated by the occurrence of several mesic-adapted terrestrial gastropods on the floodplain of the Washita River (locality 1, this study) in the absence of woody vegetation but with scattered pieces of downed wood.

FUTURE STUDIES

The finding of a substantial number of additional living species of molluscs in the Texas Panhandle raises questions as to the validity of previous environmental reconstructions based upon molluscan faunas as then known (Pierce, 1975; Neck, 1978; Johnson *et al.*, 1982; Neck, 1987a). These questions must be addressed if such reconstructions are to be considered accurate. Increased knowledge of the molluscan fauna of the area when combined with faunal surveys of adjacent areas will allow an improved interpretation of the zoogeography of the living molluscs of the Texas Panhandle.

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Appendix 1.

ADDITIONAL SPECIES RECORDS

Fossaria cockerelli (Pilsbry and Ferriss) occurs sporadically in intermittent water through most of the United States west of the Mississippi River (Hibbard and Taylor, 1960). Records of living snails in Texas were known only from Hunt and Fayette counties (Fullington, 1978:143), no closer than 550 km to this Randall County record, the site of the present record. Howver, New Mexico populations, including the type locality, are much closer to the Texas Panhandle (Bequaert and Miller, 1973). These Randall County specimens are referred to *F. cockerelli* by comparison to available drawings and photographs (Pilsbry and Ferriss, 1906; Fullington, 1978; Burch, 1982). Taxonomic relationship of *F. cockerelli* to *F. bulimoides* (I. Lea) has been unclear, but the occurrence of sympatric, non-transitional populations in Arizona (Bequaert and Miller, 1973: 197) indicates that these taxa are distinct at the species level. Fossil shells of the *F. bulimoides* group from the Texas Panhandle have been referred to both *F. cockerelli* (Frye and Leonard, 1957) and *F. bulimoides* (Taylor, 1960; Hibbard and Taylor, 1960).

Fossaria dalli (Baker) ranges from southern Canada southward to Arizona and Texas (Fullington, 1978; Clarke, 1981). Texas records are few in number but range from the humid Coastal Plain of east Texas to the Chihuahuan Desert of West Texas (Fullington, 1978). *F. dalli* is known from sites with vegetation and variable substrates in marshes, ponds, lakes, and small rivers (Clarke, 1981).

Fossaria modicella (Say) ranges from Nova Scotia to Vancouver Island southward to Alabama and southern California (Baker, 1928; Taylor, 1987). Fullington (1978) recorded no records from Texas of living *F. modicella*, a species that he synonymized under *F. obrussa* (Say) which was widespread in Texas during the Pleistocene (but not reported as living in Texas). Preferred habitats include perennial ponds, streams, and lakes as well as vernal ponds (Clarke, 1981).

Fossaria parva (Lea) has been recorded from a large geographic area from Connecticut to Alberta southward to Maryland, Oklahoma, and Arizona (Burch, 1982; Taylor 1987). Fullington (1978) reported widespread fossil occurrences but no living records of this species, which he synonymized under *F. obrussa*. *F. parva* is an amphibious species which has been reported from marshes, mud flats, lakeshores, and occasionally shallow water (Clarke, 1981).

Hebetancylus excentricus (Morlet) ranges from Central America to Texas and Florida (Basch, 1963). No previous records of living freshwater limpets (family Ancylidae) are known from the Texas Panhandle (see Fullington, 1978). The closest living population in Texas was reported from Palo Pinto County (approximately 400 km to the southeast) as *Gundlachia radiata* (Guilding) in Fullington (1978). *H. excentricus* is not known from any fossil fauna in Texas (Fullington, 1978) nor is it known from Oklahoma (Branson, 1961) or Kansas (Leonard, 1959), indicating that this species has probably icnreased its range nothward since the Late Pleistocene as water temperatures warmed. Whether the recent increase in known localities in north central Texas (McMahon and Aldridge, 1976) is due to a warming climate, increasing percentage of lotic (vs. lentic) waters, or increasing survey efforts is unknown. Preferred habitat is rock or wood substratum flowing or still waters (Fullington, 1978).

Gastrocopta tappaniana (Adams) ranges from Ontario to Maine to Alabama, Texas, Kansas, Arizona, and South Dakota. *G. tappaniana* is found in moderately mesic riparian woodlands of the Coastal Plain in eastern and central sections of Texas (Cheatum and Fullington, 1973). Presence at locality 1 indicates that ground cover and soil moisture are the primary habitat requirements. These requirements are generally provided by downed wood and leaf litter under deciduous trees, but trees may not be a primary requirement. Hubricht (1985:76) recorded *G. tappaniana* from Beckham County, Oklahoma, approximately 85 km southeast of locality 1.

Vertigo ovata (Say) ranges over most of northern and eastern North America from the Aleutian Islands to Labrador southward to Florida and eastern Texas; southwestern limit of its range is formed by Nebraska, Colorado and Arizona (Bequaert and Miller, 1973:183). Valid Texas records are known from eastern Texas, where it is "associated with considerable moisture," as far west as Dallas County (Cheatum and Fullington, 1973). Closest known living populations are in Beckham County, Oklahoma, approximately 190 km northeast of locality 3 (Hubricht, 1985). Bequaert (*In:* Bequaert and Miller, 1973) found "no reliable evidence" of living populations in the Texas Panhandle after collecting over a four year period. In the southwestern portion of its range, *V. ovata* is extremely sporadic, possibly due to chance transport via waterbirds (Bequaert and Miller, 1973). Fossil records of *V. ovata* from the Panhandle are common (Schultz and Cheatum, 1970; Johnson *et al.*, 1982; Neck, 1987a).

Oxyloma retusa (I. Lea) ranges from New England west to North Dakota and southward to Virginia and New Mexico (Metcalf in Bequaert and Miller, 1973:155; Hubricht, 1985). Typical habitat for this species includes riverbanks, pond margins, marshes, and swamps (Calkins *In:* Pilsbry, 1948; Leonard, 1959; Frest and Dickson, 1986). Previously unrecorded from Texas, *O. retusa* has been reported from Oklahoma and New Mexico (Branson, 1962; Metcalf *In:* Bequaert and Miller, 1973:155). Southern Great Plains populations of *Oxyloma* have been referred to *O. haydeni* (W. G. Binney) by some workers (Harris and Hubricht, 1982; Hubricht, 1985).

Helicodiscus singleyanus (Pilsbry) is known from various open habitats from scattered localities from New Jersey to New Mexico and Arizona (Bequaert and Miller, 1973; Hubricht, 1985). Many published records of *H. singleyanus* from the southeastern United States refer to other species of the subgenus *Hebetodiscus*, including *H. inermis* which is also known from the Texas Panhandle.

Hawaiia minuscula (A. Binney) has a native range that covers much of the Western Hemisphere from Newfoundland to Alaska south to Central America and the West Indies; subsequently, this species has become almost cosmopolitan due to spread by human activity (Bequaert and Miller, 1973). Leonard (1959) reported *H. minuscula* under rocks and wood as well as in grass clumps in both bottomland and upland environments.

Zonitoides arboreus (Say) ranges throughout the United States from coast to coast, although there is a large gap in the Great Plains where the lack of trees provides few areas of suitable habitat. The nearest records to Buffalo Lake National Wildlife Refuge are Cimarron County, Oklahoma; Wichita County, Texas; and San Miguel County, New Mexico (Hubricht, 1985). In the southwestern United States, *Z. arboreus* is native at higher elevations (up to 3650 m); below 1525 m it occurs generally only as temporary adventive populations (Bequaert and Miller, 1973:88). *Z. arboreus* is a common urban species (Hubricht, 1985:32), including the Southern High Plains of Texas (Neck, 1989a).

Euconulus trochulus (Reinhardt) has a broad geographic range from southern Canada to the Gulf coast westward to the Great Plains. This taxon has long been considered a subspecies of *E. chersinus* (Say), but Hubricht (1983) raised *trochulus* to specific status. Texas records are generally from the Coastal Plain (Hubricht, 1985). In the Texas Panhandle, *E. trochulus* lives in narrow, protected canyons with leaf litter and moist sandy floodplains with protective cover.

Anodonta imbecillis Say ranges from southern Ontario to Georgia and westward to the northern Great Plains and northern Mexico (Clarke, 1981), where it is found in a variety of waterbodies from ponds to small rivers and lakes on mud or sand substrates (Clarke, 1981; Neck, unpub. data). Native range in the Red River of the South extends as far west as the Wichita Falls, Wichita County area (Neck, 1989b). Occurrence of *A. imbecillis* in Lake Meredith (locality 8) is due to human introduction.

Musculium transversum (Say, 1829) ranges from Quebec to the Northwest Territories southward into Mexico (Clarke, 1981). Usually found in mud (but occasionally in sandy substrata), *M. transversum* is known from sloughs, lakes, and rivers (Herrington, 1962). I have collected this species in central Texas usually from moving water or ponds with freshwater input (Neck, unpub. data).

Pisidium casertanum (Poli) is found in almost all of the Western Hemisphere, ranging from Alaska to Patagonia (Hibbard and Taylor, 1960). This species inhabits lakes, ponds, streams, swamps, and even temporary water habitats (Herrington, 1962; Clarke, 1981).

Pisidium compressum Prime ranges over most of North America from the Northwest Territories southward through the United States to Mexico (Herrington and Taylor, 1958). *P. compressum* can be found in lakes, rivers, and creeks but never in swamps, lagoons, or bog ponds (Herrington and Taylor, 1958), although Clarke (1981) stated that its usual habitat is in shallow water among vegetation.

Pisidium nitidum Jenyns has a Holarctic range and is found over most of North America except for the southeastern United States (Hibbard and Taylor, 1960). *P. nitidum* can survive in almost any perennial body of water, but is usually found in shallow water (Clarke, 1981).

Pisidium punctiferum (Guppy) ranges from southern Canada to Uruguay with additional records from Europe (Herrington, 1962). *P. punctiferum* is known from creeks, rivers, and lakes according to Herrington (1962), who reported this species from unspecified locations(s) in Texas.